BREEDING BIOLOGY AND POPULATION DYNAMICS OF THE WEDDELL SEAL, *LEPTONYCHOTES WEDDELLI* : A REVIEW

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ABSTRACT

A brief review of the breeding biology of the Weddell seal, *Leptonychotes weddelli* is presented, with a discussion of factors which regulate the sizes of the populations.

In early spring breeding colonies form on sea-ice as pregnant females haul out in areas of perennial cracking. The period between hauling out and birth of the pup, a time of fasting for the female, apparently increases in length with latitude and is generally later at higher latitudes.

Development of the single pup is rapid; it doubles its weight in 10 days and reaches 114 kg weight before weaning at 6 to 7 weeks of age. Twinning is rare. The lanugo of the pup provides insulation in the absence of blubber and allows the pup to survive at temperatures well below freezing. Mortality of pups, highest in the first week of life, is largely determined by climatic and physical factors. The pup's diving and swimming proficiency develops fairly rapidly but appears to necessitate a transitional crustacean diet following weaning. Weaning at high latitudes is thought to be timed to coincide with the summer phytoplankton bloom.

The parent-offspring bond, initially strong, is broken about 50 days after birth and pups are forced, through strong competition with adults for food, to retreat towards the pack-ice. In breeding colonies seals are spaced wider than at other times on the sea-ice because of territorial behaviour. Both sexes defend aquatic territories while breeding but there is little fighting.

Populations of *Leptonychotes* exist as discrete units. Food is probably the ultimate factor limiting population size but other important factors are the availability of breathing holes and the ability to maintain these. Intra-specific and intra-sexual strife are also significant. Ice stability can have large effects on pupping success. Predation may be important in some areas but is poorly documented.

INTRODUCTION

The Weddell seal, *Leptonychotes weddelli*, is probably the most abundant and best known of the Antarctic pinnipeds. It was first discovered by James Weddell in 1823 and was described by Lesson in 1826 from the type specimen collected by Weddell.

This seal is circumpolar in distribution being found mainly in fast ice areas off the Antarctic continent (Stirling 1969a). While it has often been observed in the pack ice, it is not abundant there. It is common in the South Orkneys but less numerous in South Georgia where a small colony forms the northern breeding limit of the species (King 1964). The southern breeding limits extends to within 10 degrees of the South Pole (Kooyman 1969). Occasional sightings have been made in South Australia

(Iredale and Troughton 1934), New Zealand (Turbott 1949), Uruguay (Vas Ferriera 1956) and at Macquarie, Heard, Falkland and Kerguelen Islands (King 1964).

BREEDING BIOLOGY

Towards the end of August (in McMurdo Sound) pregnant females haul out onto the sea-ice in areas of perennial cracks to form groups or breeding colonies (Stirling 1968). The cracks which first develop in spring, and probably those present during winter, become the sites of colony formation regardless of such factors as prevailing winds and drift snow accumulation (Stirling 1968). Females with pups generally move from exposed areas into more sheltered places when cracks become available (Stirling 1968). Although it is known that the Weddell seal can maintain holes in the ice by abrading with the canine teeth (Wilson 1907, Lindsey 1937, Bertram 1940, Stirling 1969a, Kooyman 1969), breathing and exit holes are usually made by enlarging cracks formed by glacial movement or tidal action (Stirling 1969a).

Observations on tagged individuals indicate that females tend to return to the same colony to pup in successive years. If they fail to return to the colony occupied the previous year, then they appear to enter the colony closest to it (Stirling 1968). It is thought that adults return to the site of nativity to reproduce (Stirling 1969a).

At Signy Island pupping occurs about 27 hours after the female hauls out in the breeding colony (Mansfield 1958), but at McMurdo Sound the females haul out about a week before parturation (Caughley 1959, Smith 1966). Solitary pupping occurs only occasionally (Stirling 1969a). Birth occurs on the sea-ice from September to November, the date of occurrence being later at higher latitudes (Stirling 1969a). Seals younger than 3 years generally do not breed and the pregnancy rate of 3 and 4 year old females was lower than older age classes (Stirling 1968).

Birth itself takes about 15 minutes. The newborn pup opens its eyes almost immediately and is able to move about over the ice (Mansfield 1958). A marked increase in the aggressiveness of the cow occurs following the birth of the pup but this declines progressively as the pup develops (Mansfield 1958). At birth the single pup weighs from 27 to 30 kg and is about 1.4 m long. Growth is extremely rapid: the pup doubles its weight after 10 days and, when weaned at 6 to 7 weeks of age, it has reached a weight of about 114 kg (Lindsey 1937, King 1964, Stirling 1968). Lindsey (1937) found that this increase of about 85 kg in the pup is correlated with an estimated 140 kg decrease in the weight of the female, approximately 65 kg of which represents losses of skin and blubber. This highly efficient transfer from mother to pup takes place through the milk which contains between 42.5 and 72.8 percent solids (Kooyman and Drabek 1968). As lactation proceeds the milk becomes more concentrated as the fat content increases and the volume produced drops off sharply during the two weeks before weaning (Kooyman and Drabek 1968).

Only one probable case of live twins has been reported (Stirling 1971) and, although twins in utero have been found

(Lindsey 1937, Bertram 1940, Smith 1966, Stirling 1968), twinning is thought to be very rare (Stirling 1968). Occasionally two pups, one fat and one thin, may be seen with the same female (Stirling 1968, D. Greenwood pers. comm.). The thin pup has either been abandoned or its mother has died. Sometimes these pups suckle successfully but whether they ever reach weaning is not known.

The lanugo of the Weddell seal pup, about 20 to 25 mm deep, is made up of very dense, flat, wavy hairs (Ray and Smith 1968). Short hairs of the juvenile coat are present from birth and are exposed by the loss of lanugo. On average the moult begins about two weeks after birth and is complete four weeks later, revealing the juvenile coat which closely resembles that of the adult (Mansfield 1958, Ray and Smith 1968). Initially pups lack the thermal insulation of blubber and the lanugo has been evolved to overcome this. It is effective as an insulator only when dry and thus the pups in lanugo are better adapted to temperatures well below freezing. At temperatures close to or above 0°C the coat becomes wet and loses its effective insulatory properties. For this reason, pups born early in the season will have a better chance of survival than those born later when conditions are warmer and wetter (Ray and Smith 1968). The pup has an extremely high metabolic rate, higher than any other seal yet tested, which, along with the lanugo, allows the pup to tolerate temperatures as low as -30°C (Ray and Smith 1968). A further thermoregulatory mechanism found both in the juvenile and the adult, is the skin's ability to absorb solar radiation. This is facilitated by the nature of the hair itself which creates a lenticular effect and a "greenhouse" effect to trap heat (Ray and Smith 1968). Basking on clear days orientated at right angles to the sun also serves to increase heat absorption (Ray and Smith 1968).

Male pups slightly but consistently outnumber female pups, but the sex ratio at birth does not differ significantly from unity (Lindsey 1937, Bertram 1940, Mansfield 1958, Smith 1966, Stirling 1968). Mortality of pups prior to weaning has been investigated intensively (Mansfield 1958, Stirling 1968). Results show that in a normal season at McMurdo Sound there is about a 5 percent mortality up until weaning and that the majority of these deaths occur during the first week of life. Lindsey (1937) reported pup mortality in the Bay of Whales as 18 percent, and Mansfield (1958) considered that it would generally be lower at the South Orkneys. In a season of early ice break out at the latter location, pup mortality at one colony was estimated at 30 to 50 percent (Mansfield 1958). This illustrates just how drastic the effects of unstable ice conditions can be. More recently Smith and Burton (1970) have made an estimate of pup mortality of about 5 percent at the South Orkney Islands in a normal season. The main cause of death before weaning is probably through pups getting into cracks they cannot get out of and, as a result, getting crushed by ice, frozen in or drowned (Stirling 1968). Predation on pups by leopard seals (*Hydrurga leptonyx*) and killer whales (*Orcinus orca*) may occur but has not been recorded.

Pups first enter the water at 8 to 10 days of age and, accompanied by its mother, each pup learns to swim competently

(Lindsey 1937, Mansfield 1958, Caughley 1959). During the first few days following its initial swim, the pup does not remain in the water for more than 15 minutes at a time (Caughley 1959). The mother often has to assist the pup in leaving the water by lifting with her head from underneath (Stirling 1968). It submerges for no more than a few seconds and hence does not swim under the ice. By its fifth day of swimming the pup has gained sufficient strength and ability to spend long periods under the ice either by itself or accompanied by its mother (Caughley 1959). Diving proficiency has been found to develop very rapidly in the pup (Kooyman 1967). Observations made on 7 week old pups showed that they could remain submerged for over 5 minutes, make dives to depths greater than 90 m and in some cases even capture fish (Kooyman 1967).

Following weaning, while their diving abilities improve, the pups go through a transition period during which their food consists largely of crustaceans (Lindsey 1937, Bertram 1940). It is thought that the crustacean diet is necessitated by the pup's relative inefficiency in capturing fish which make up the bulk of the adult diet (Dearborn 1965). The peak of the summer phytoplankton bloom occurs in McMurdo Sound at about the same time as weaning takes place (Bunt 1964). Stirling (1968) suggests that breeding has evolved to coincide with this event in order that pup survival may be enhanced by an abundant food supply.

The parent-offspring bond, very strong at first (Mansfield 1958), is thought to begin weakening from the first time the pup swims under the ice alone (Caughley 1959), and that it is completely broken about 50 days after birth (Lindsey 1937, Caughley 1959). For the rest of the summer a few pups remain in the small areas of fast ice close to shore (Stirling 1968), but little is known of their general movements after weaning. Claims that they migrate out of the breeding areas to the edge of the fast ice and pack ice where they over-winter and spend the first one to three years of their life have been made (Smith 1966, Kooyman 1967), but the general absence of these age classes from inshore areas is well known (Caughley 1959, Smith 1966, Kooyman 1967, Stirling 1968).

On entering the breeding colony the female Weddell seal defends an aquatic territory which is relatively poorly defined (Ray 1967). Wider spacing on the sea-ice than at other times is characteristic of breeding colonies at this stage (Stirling 1969a), and the females become aggressive towards any intruders, human or seal (Mansfield 1958, Stirling 1968). Pregnant females form large groups and make up about 70 percent of the seals present in the colony. Non-breeding females and males make up the remaining 30 percent (Stirling 1969a). Males also defend aquatic territories but these are larger and more well defined than those of the female (Ray 1967, Kooyman 1967). The sex ratio of seals in the pupping colony at this stage is 6 or 7, and up to 10 females per male, but is about 2 to 4 females per male outside the breeding areas (Stirling 1969a). Males usually occur singly or in groups of 2 or 3. Sub-adult seals are largely excluded from the breeding colonies but occur in small numbers around cracks away from the colonies (Stirling 1969a).

Defence of territories is vigorous, especially between males, and evidence of fighting - fresh cuts inflicted by seal teeth - is seen on most adults at this time (Mansfield 1958, Lindsey 1937, Bertram 1940, Smith 1966, Stirling 1968). It is thought that about 40 percent of wounds to the adult Weddell seal are incurred during intra-specific encounters (Smith 1966), however the number of wounds and scars on females is very small in comparison with that on males (Lindsey 1937, Bertram 1940, Smith 1966). Intra-sexual fighting between females although rare, does occur (Lindsey 1937, Bertram 1940). These fights have been observed to occur when a female, with or without a pup, comes too close to a breeding female. It has been concluded (Bertram 1940) that the amount of fighting among Weddell seals is not great and is negligible when compared with the fighting which occurs between males of polygamous species. Little is known about the selection of mates or development of harems but existing evidence provides strong support for the contention that the species is polygamous (Stirling 1968).

The female does not feed or enter the water from the time she hauls out before pupping until about six days after the event (Caughley 1959); thus she fasts for about thirteen days which spans pupping and the first few days of suckling. When this fast is broken, the periods spent away from the pup are initially less than an hour long, but are extended up to four hours within a few days (Caughley 1959).

Although the details of mating are not well known, it appears that females with pups ovulate soon after the cessation of lactation and mating occurs at this time (Smith 1966). It is not known whether ovulation is spontaneous or stimulated by copulation. Implantation of the blastocyst is delayed for a period of from two to eight weeks (Smith 1966), thus giving a gestation period of about ten months. Copulation has been observed only once (Cline et al. 1971); it occurs in the water beneath sea-ice. Females which have missed breeding mate before the majority of pups are weaned (Smith 1966).

The pups are weaned and females mated by mid-December at McMurdo Sound (Smith 1966), and as this occurs territorial behaviour largely breaks down (Stirling 1968).

POPULATION REGULATION

Populations of Weddell seals are thought to exist as discrete units with only limited emigration and immigration (Stirling 1968). Evidence for this comes from resightings of large numers of tagged individuals in McMurdo Sound (Stirling 1968), and in part from analyses of gene frequencies of three blood serum transferrins in seal populations at three widely spaced localities around the Antarctic continent (Shaughnessy 1969).

Several factors may be important in regulating the sizes of stable populations. Food is probably the ultimate factor which would limit the expansion of a population (Stirling 1968), but does not appear to be limiting in any population so far studied. The availability of breathing holes during winter may limit the numbers remaining near pupping colonies over this period, but would probably not limit the size of the population as a whole because cracks appear to be common in the more seaward annual ice (Stirling 1968). However the ability to maintain breathing holes over winter is considered to be an important mortality factor (Mansfield 1958, Stirling 1969b). Weddell seals can keep breathing holes open during winter by abrading the sea-ice with their teeth (Bertram 1940, Wilson 1907, Stirling 1969b). Stirling (1969b) found that continual abrasion gradually wears the teeth down and they occasionally fracture. Wear down to the pulp cavity with subsequent abcess development is not uncommon. This condition may seriously affect a seal's ability to maintain a breathing hole and eventually lead to its death (Bertram 1940, Stirling 1969b). Tooth wear was found to increase fairly rapidly in individuals older than the mean age of the population (Stirling 1969b). From this evidence it has been concluded that tooth wear may be a significant mortality factor in adult seals (Bertram 1940, Stirling 1969b).

The mortality rate of adult males is higher than for adult females, probably a consequence of male territorial fighting during breeding seasons (Stirling 1968). Territorial behaviour by both sexes will tend to limit the number of seals breeding at any one colony, and thus further limit the population size (Kooyman 1967, Stirling 1968). The significance of intra-specific and intra-sexual fighting as mortality factors in the Weddell seal is not properly known. Smith (1966) made a detailed study of injuries to the species but failed to comment on the significance of those incurred during intra-specific encounters as a mortality factor. Among males only, intra-specific fighting is thought to be an important cause of mortality (Stirling 1968).

Early break out of sea-ice may have a large effect on the survival of pups; at Signy Island such an event is thought to have resulted in a 20 to 35 percent mortality of pups before weaning (Mansfield 1958). Under conditions of crowding in breeding colonies social stress may retard reproduction considerably (Stirling 1968). A facultative delay in the attainment of maturity may occur when ecological factors permit populations to reach maturity (Stirling 1968).

Disease has not been regarded as contributing significantly to mortality of the Weddell seal (Stirling 1968), although an epizootic in crab-eater seals was reported to have eliminated 85 percent, on average, of infected populations (Laws and Taylor 1957). Resident Weddell seals, dogs and men were not affected by this disease.

Predation by killer whales (*Orcinus orca*) on the Weddell seal appears to be significant in some areas. Bertram (1940) described a distinct wound pattern inflicted on crab-eater seals by *Orcinus*, and this type of wound has been observed on Weddell seals when killer whales have been in the area (Smith 1966). More direct evidence that killer whale predation on *Leptonychotes* may be important in some areas comes from records of killer whale stomach analyses. One killer whale taken off the Pribilof Islands had 32 adult seals in its stomach (Slijper 1962). Walker (1964) described the stomach contents of one which contained 24 seals, and another which contained 13 porposes and 14 seals. In populations near open water or inhabiting pack ice, predation by this large mammal must be considered as a potentially serious mortality factor (Stirling 1971).

The leopard seal, *Hydrurga leptonyx*, has been suggested as a potential predator of Weddell seals (Trouvessart 1907, Anderson 1905, Wilson 1907, Bruce 1913, Stirling 1971), but no evidence indicating attacks on juveniles or adults has been documented (Smith 1966). The leopard seal could well be responsible for the deaths of some pups and sub-adults (Stirling 1971).

Crushing between blocks of ice may occur in areas of pack ice but is rare in fast ice (Stirling 1968). However very large blocks of ice splitting off glaciers and falling into breeding colonies have been observed (personal observation) and may be responsible for the deaths of several pups and adults.

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